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Being at the mercy of their food: What kind of prey do Ural owls (*Strix uralensis*) deliver at the nest in a year with low vole abundance, and when do they deliver what?

Å være prisgitt sin mat: Hva slags type byttedyr leverer slagugler (*Strix uralensis*) på reiret i et år med lav forekomst av smågnagere, og når leverer de hva?

Ane Guro Moen

ACKNOWLEDGEMENTS

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Ås, May 2015

Ane Guro Moen

ABSTRACT

The prey deliveries at five nests of the Ural Owl (*Strix Uralensis*) were studied in Värmland county in Sweden over a period of 42 days in May-June in the low-vole year 2008 by using video camera mounted inside the nest box. The camera allowed prey identification of 187 prey items and made it possible to determine the handling of 163 of these. Of the prey items recorded delivered, mammals were by the most abundant prey both by number (53 %) and mass (59 %), followed by birds (26 % by number and 33 % by mass), amphibians (12 % by number and 7 % by mass), insects (2% by number and negligible by mass) and common lizard (Zootoca vivipara; <1 % by number and negligible by mass). Among the mammals, common shrew (*Sorex araneus*) was the most important prey by number and mountain hare (*Leptus timidus*) the most important by estimated mass. The predicted overall prey delivery rate was larger during night than during day. The delivery rate of birds had a higher peak during the night and lower level during the day than the delivery rate of mammals. The latter showed a similar diurnal pattern for voles and shrews. The female handled 42 % of the prey items alone by feeding the nestling, whereas the nestlings handled the remaining prey item unassisted. The probability that the nestlings handled prey unassisted increased with nestling age and decreased with prey mass, and was lower for avian prey than for mammals and amphibians, but did not differ between mammals and amphibians.

SAMMENDRAG

Byttedyr levering hos fem hekkende par av slagugle (*Strix uralensis*) ble studert i Värmland, Sverige over en periode på 42 dager i mai-juni i et dårlig smågnager år 2008 ved hjelp av videokamera montert på innsiden av reirkassen. Kameraopptakene tillot identifikasjon av 187 byttedyr og gjorde det mulige å bestemme håndteringen av 163 av disse. Av byttedyrene registrert levert til reirkassene, var pattedyr den mest tallrike byttedyrtypen både i antall (53 %) og masse (59 %), fulgt av fugler (26 % i antall og 33 % i masse), amfibier (12 % i antall og 7 % i masse), insekter (2 % i antall og uvesentlig i masse) og firfisle (Zootoca vivipara; <1 % i antall og uvesentlig i masse). Blant pattedyrene var vanlig spissmus (*Sorex araneus*) det viktigste byttedyret i antall, og hare (*Lepus timidus*) det viktigste i vekt. Leveringsraten av byttedyr totalt var høyere gjennom natten enn gjennom dagen. Leveringsraten av fugler hadde en høyere topp i løpet av natten og lavere nivå i løpet av dagen enn leveringsraten av pattedyr. Hunnen håndterte 42 % av byttedyrene alene ved foring av ungene, mens ungene håndterte de resterende byttedyrene alene. Sannsynligheten for at ungene håndterte byttedyr alene økte med ungenes alder og avtok med byttedyrets vekt, og var lavere når byttedyret var fugl enn når det var pattedyr eller amfibium, men ikke forskjellig for pattedyr og amfibium.

CONTENTS

1 INTRODUCTION

Natural selection is one of the key processes in nature and favors individuals that produce the maximum number of reproducing offspring in a lifetime (Krebs 2001). How many offspring an organism can produce during its lifetime depend on reproductive effort, which is the proportion of total energy and nutrients that an organism allocates to reproduction, the remaining energy and nutrients are used for maintenance and survival of the parent (Martin 1987). Behavior that allows animals to exploit food sources efficiently creates possibilities for increased reproductive effort (Krebs 2001).

The ecology and behavior of a species are affected by its activity rhythm (Erkert & Kappeler 2004). In classic ecological theory, circadian activity rhythms are part of the adaptation to the environment, reflecting the adjustments in an animal´ physiology and behavior to trade-off the diet changes in different environmental conditions (Beltrán & Delibes 1994; Erkert & Kappeler 2004). To either be diurnal or nocturnal reflects a type of niche differentiation, where different species niches are not defined by utilizing different resources, but by the time of day these resources are utilized (Kronfeld-Schor & Dayan 2003).

Birds adjust their reproductive effort to fluctuating availability of food (Lack 1968; Hirshfield & Tinkle 1975), either depending on the provisioner's working capacity (Ydenberg 2007) or the provisioning parent´s need to alter its feeding behavior in relation to prey available (Steen 2004). In raptors, the type of prey available, influences the time required and energy spent by the parent to capture, prepare, self-feed on the prey or provide it for the nestling (Slagsvold & Sonerud 2007; Steen 2010; Steen et al. 2011). Many raptors at northern latitudes depend on microtine rodents as their main prey and they continue to hunt these during reproduction. However, the population density of these rodents varies considerably between years and across Fennoscandia shows a 3-5 years cyclic pattern in their population numbers (Hansson & Henttonen 1985; Hanski et al. 1991; Korpimäki & Krebs 1996). The temporal and spatial synchrony between the population size of microtine rodents and small game may be explained by varying impacts of generalist predators surviving on both rodents and small game (Hagen 1952; Lack 1954). Angelstam et al. (1984) predicted that the collection of generalist predators synchronizes their own reproduction to the population fluctuations of their main and alternative prey groups. In peak microtine rodent years, the predation pressure on alternative prey species is relaxed, and these prey species enjoy high survival rates and increase in numbers. As microtine rodent populations decline, predators switch to the less abundant alternative prey species whose survival rates in turn are lowered (alternative prey hypothesis, Angelstam et al. 1984; Hanski et al. 1991).

The Ural Owl is a large, resident and a K-selected avian predator (Korpimäki 1986) using auditory prey location and the sit and wait travel strategy during hunting (Cramp 1985). It is a cavity nester that readily accepts special made large nest boxes for breeding. Compared with other *Strix* species, the Ural Owl is intermediate in circadian activity pattern (Korpimäki 1986). Ural owls are also active during the day, especially in the morning (Korpimäki & Sulkava 1987). The diet of Ural owl is varied and the species is therefore regarded as a food generalist (Lundberg 1979; Korpimäki & Sulkava 1987).

Ural Owls display female-biased sexual size dimorphism; the mean body mass for a female is approximately 871 g, while for male it is only 720 g (Mikkola 1983; Brommer et al. 2003). Ural Owls have separate sex-roles, where the female incubates, broods, and feeds the nestlings, while the male hunts for prey that he provides for the females and the nestlings (Cramp 1985). The pair is resident in their territory for life (Lundberg 1979; Saurola 1987).

The reproduction and survival of Ural Owls are strongly influenced by the access to potential prey species (Lundberg 1979; Newton 1979; Korpimäki & Sulkava 1987). Diet and prey selection of the Ural Owl has been extensively studied in Sweden and Finland in recent years (Lundberg 1981; Jäderholm 1987; Korpimäki & Sulkava 1987; Brommer et al. 2002a; Brommer et al. 2002b; Brommer et al. 2003; Karell et al. 2010; Lehikoinen et al. 2011). *Microtus* voles are considered the primary prey of Ural Owl, whereas water vole (*Arvicola terrestris*), bank voles (*Clethrionomys glareolus*), common shrew (*Sorex araneus*) and a variety of birds are considered as alternative prey types (Lundberg 1981; Korpimäki & Sulkava 1987; Rønning 2007). The number of young Ural owls produced annually vary greatly between years and in synchrony with the population fluctuations of *Microtus* voles (Korpimäki & Sulkava 1987). Ural owls invest most in reproduction during the increase and peak phases of the vole cycle (Lundberg 1981; Jäderholm 1987; Korpimäki & Sulkava 1987; Sidorovich et al. 2003).

In this thesis, I have analyzed video recorded in 2008 in five Ural owl nests to determine the diet and prey handling during the nestling period. Previous studies have explored the diet of the Ural Owl by analyzing prey remains from nests and from pellets found near nests. However, this method has probably given a too narrow view of the diet. The reason for this is that females remove prey remains from the nest (Korpimäki & Sulkava 1987), and that some prey items do not leave traces behind. Rønning (2007) used video cameras placed in the nest box to observe prey deliveries, which provided new insight into how the female feeds the nestlings and how different types of prey are handled.

In particular, I wanted to answer the following questions: 1) What is the prey delivery rate of providing Ural Owls, and at time of the day do the delivered prey items arrive? 2) How much food do the nestlings consume? 3) What affects whether the female feeds her nestlings or the nestlings feed unassisted?

Because this study includes data from a year with a low rodent population, I expected a high proportion of alternative prey in the owl´s diet.

2 METHODS

2.1 *Study area*

The five nests of Ural owls from which data were collected were in nest boxes located in Värmland county in Sweden (60°13´- 60°21´ N; 12°52´ - 13°16 E). The study area is dominated by boreal coniferous forest, intercepted by large areas of bog and mire, and with negligible patches of farmland (Nilsson 1990).

The nests were video monitored from 18 May to 13 June 2008, by Gunnar C. Nyhus. As a part of the video monitoring of the nest boxes, the date of egg laying, clutch size, hatching date and number of hatched young was registered. In addition, the female and each nestling were ringed. Brood size varied from one to three nestlings, but two of the nine nestlings that hatched died during video monitoring, so that brood size during monitoring varied from one to two (Appendix 1).

To estimate the food supply for the Ural owls, small mammals were snapped-trapped in the study area by Geir A. Sonerud in May 2005-2008. The trapping index (pooled for shrews (Soricidae), field vole (*Microtus agrestis*) and bank vole (*Myodes glareolus*), and dominated by the latter) was lower in 2008 than in 2007 and 2006, but not lower than in 2005. Thus, in 2008 the small mammal populations available for the Ural owls were at a low level after a peak in 2006-2007. The number of Ural owl nests in the study area varied accordingly (Gunnar C. Nyhus, pers. comm.). In 2004 apparently there was a crash in the small mammal populations, because no breeding pair of the Ural owl was recorded in the 250 nest boxes available in the study area. In 2005 two nestings were detected in the boxes, and in 2006 seven, followed by no less than 21 nestings in 2007. In 2008, the number of nestings in the boxes dropped to nine (Gunnar. C. Nyhus, pers.comm.).

2.2 *Video Recording*

In the present study, an automated video monitoring system was used. The system consisted of a CCTV camera (Watec LCL-903HS Camera Module connected to a camera lens (Cosmicar/Pentax LX CS 2.8mm 1:1.2)) and a Digital video recorder (DVR). The camera was mounted on the inside of a specially designed roof for the nest box, which temporarily replaced the original roof. The camera was pointed towards the nest box entrance, and the nestlings did not block the view of the delivering prey. The nest boxes had been installed c. 10 m above ground and a 30 m video cable was connected to a waterproof Zerges box placed on the ground located c. 20 m from the nest tree. The box contained the DVR and a DC converter, connected to a 12 V lead battery providing power (Figure 1). The battery was replaced every second day. The reason for placing the recording equipment some distance from the nest tree was to minimize the well-known aggressive nest defense behavior of the Ural owl female (Kontiainen et al. 2009), which may cause rough meetings, where the female Ural owl may hit a human intruder with force, posing a risk that the female can hurt herself as well as inflict wounds on the human disturber (Kontiainen et al. 2009).

Each of the five nests included in the study was video monitored between 5 and 13 days, in total 42 days. The activity in the five nests was monitored around the clock, and the DVR detected movement in the area around the nest entrance (video motion detection sensor). By detection of movement the DVR automatically stored the event. In addition to the event, it also stored 10 s prior to the triggering. This ensured that all records of prey deliveries included 10 s before the triggering, allowing a view of the incoming flight by the delivering parent, and thus made it easier to identifying the prey items it carried. For a triggered event, the recording lasted about 45 s.

The total duration of the recorded activity at the nests was 992 hours. This recorded video was later analyzed by connecting the DVR to a TV monitor in the lab.

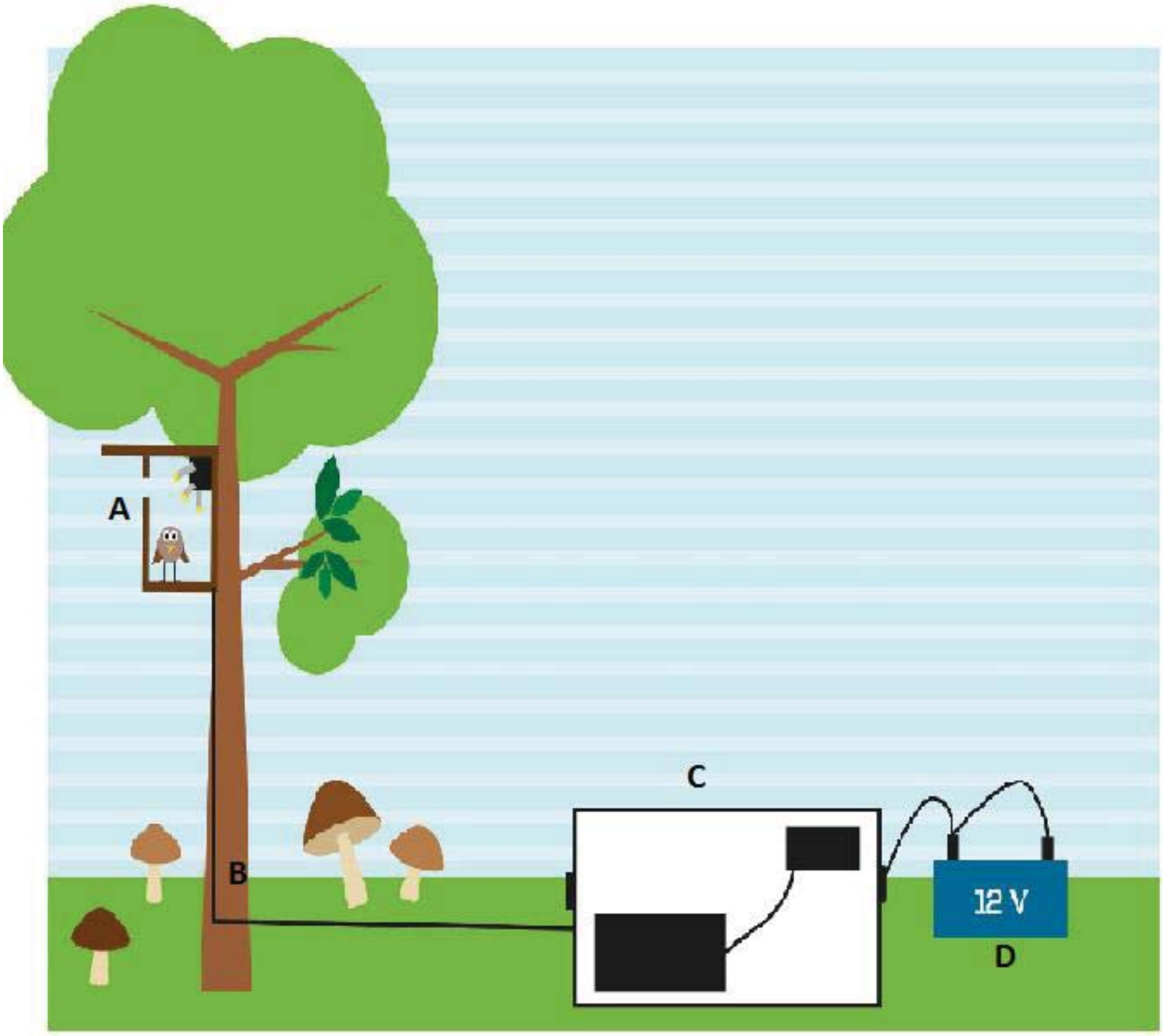

Figure 1: An illustration of the monitoring system: (A) nest box on a tree, with a led lens camera, (B) video cable (30 m), (C) waterproof Zergas box, containing the DVR and the DC converter, and (D) power supply.

2.3 *Prey deliveries and identification*

For each recorded prey delivery at the nest, I noted the sex and behavior of the delivering parent, including time of arrival and departure from the nest.

For each prey delivery, the prey item was identified, and the handling behavior was scored as whether the nestlings ingested the prey item unassisted or was fed and assisted by the female. Additionally I registered whether the prey item were delivered decapitated, partly eaten or plucked.

The age of the nestlings was estimated based on the method used by Kontiainen et al. (2010), i. e. assuming that the eggs are laid by two days interval, that incubation does often not begin until after 3 eggs are laid, that incubation time per egg is 32 days, and that hatching takes two days (Kontiainen et al. 2010). The estimated date for the first eggs laid (Gunnar C. Nyhus, pers. comm.) could therefore be used to calculate the hatching date, and thus the nestling age at each prey delivery.

The image quality of the video recording enabled identification of most prey. Video recordings were in color if the light conditions allowed, and recordings from nighttime were in black and white due to the IR light function. Small mammals were identified from body size, head shape, fur structure and tail length. The prey items recorded delivered were identified to species, but if species identification was uncertain, the prey item was instead assigned to prey group (*Turdus, sp*., *Anthus, sp*. and Coleoptera, *sp*.). Some of the prey items were not possible to identify, due to absence of visual information on the video, e.g. the female blocked the camera view, or the prey item had been partly consumed or decapitated.

In some cases the female arrived at the nest box with a prey item without providing it for the nestling and instead flew off with it (n = 5). These prey items were included in the predicted prey body mass delivered to the nest boxes, but excluded in the further analysis.

2.4 Estimates of prey body mass

The body mass of small mammals, common lizard (*Zootoca vivipara*) and common grass frogs (*Rana temporaria*) has a quite high intra specific variation (Steen 2010). However, rather than to estimate the body mass of each small mammal, lizard and frog delivered from its size on the video frame, as done by Kristiansen (2003) and Steen (2010), an average body mass for each species was assigned. This allowed assigning a body mass to a prey item without having to see its whole body. For the incomplete four juvenile mountain hares delivered, the mass was estimated to be 15 % of the mean body mass of a juvenile mountain hare (Bray et al. 2002). For decapitated mammals (n=5) and birds (n=5) I subtracted 16.5 % of the body mass for the mammals (Asakskogen 2003), and 12.8% for the birds (see Sonerud et al. 2014a for details).

Adult birds have a relatively small intra-specific variation in body mass (Sonerud et al. 2013), and for that reason, I used a mean value taken from the literature (Cramp 1985; Cramp 1988; Cramp 1992; Selås 2001; Svensson et al. 2011) for all items of the same bird species. If an avian prey was identified as a juvenile, as often was the case for thrushes (*Turdus*), 80 % of the adult bird body mass of the possible species was used as an estimate. The remaining juvenile birds were assigned the same body mass as adults (Steen 2010). Unidentified avian prey items were assigned to two groups, either small birds or large birds, based on size observed at delivery. For plucked avian prey it was difficult to make a precise estimate of the plucking degree from the video recording. Therefore I did not subtract any mass for the birds delivered plucked.

All insects delivered to the nestlings were of the same size. Data on body mass of insects were obtained from Itämies og Korpimäki (1987), who assigned insects taken by the Eurasian kestrel (*Falco tinnunculus*) a body mass of 0.2 g.

Of the 187 prey items delivered, ten were too difficult to identify to species or group, so I used the mean body mass of the 177 identified prey items to estimate body mass for the 10 unidentified prey items.

2.5 Statistics

In order to analyse the prey delivery and prey handling of the Ural owl, I used linear and generalized linear-mixed-effects models in the "MASS" and "LME4" package in the statistical software R, version 3.10.0. (R Development Core Team 2014). Breeding pair ID was included as a random effect to control for repeated measurements of the same breeding pair and any inter-pair variation (Pinheiro & Bates 2000).

To analyze daily activity rhythms around the clock I used the cosinor method for the explanatory variable "time of the day", i.e. 0 to 24 hours (Nelson et al. 1979; Pita et al. 2011). I tested the 24 hours period, where each hour-block was the sample unit. I used logistic regression (binomial distribution) to obtain probabilities of prey deliveries as function of "time of the day", with the response variable being defined as whether there was any prey delivery or not (i.e. "yes" or "no") within a given hour-block. The activity models were specified as follow:

$$\mathrm{M}_0\text{: } logit\big(f(x)\big) = a_0 + \mathcal{E}$$

$$\mathrm{M}_1\text{: } logit\big(f(x)\big) = a_0 + \left(a_1 \cos\frac{2\pi x}{24} + b_1 \sin\frac{2\pi x}{24}\right) + \mathcal{E}$$

$$\mathrm{M}_2\text{: } logit\big(f(x)\big) = a_0 + \left(a_1 \cos\frac{2\pi x}{24} + b_1 \sin\frac{2\pi x}{24}\right) + \left(a_2 \cos\frac{2*2\pi x}{24} + b_2 \sin\frac{2*2\pi x}{24}\right) + \mathcal{E}$$

$$\mathrm{M}_3\text{: } logit\big(f(x)\big) = a_0 + \left(a_1 \cos\frac{2\pi x}{24} + b_1 \sin\frac{2\pi x}{24}\right) + \left(a_2 \cos\frac{2*2\pi x}{24} + b_2 \sin\frac{2*2\pi x}{24}\right) + \left(a_3 \cos\frac{3*2\pi x}{24} + b_3 \sin\frac{3*2\pi x}{24}\right) + \mathcal{E}$$

"Time of the day" is expressed by x, and $\mathcal{E}$ is the random effect "breeding pair ID". Each model fit (M_1-M_3) was evaluated by assessing AICc values (Akaike 1978) compared with a model including only the random term (M_0). The model fit was ranked in accordance with the AICc values, with a difference in AICc (ΔAICc) from the best model of 2.0 as the critical value for separating the model with the best fit (Burnham & Anderson 2002).

Further, I tested the probability that the nestlings fed on the prey unassisted. The response variable was defined as whether the female was feeding dependent nestlings or nestling were feeding unassisted, while explanatory variables were prey mass and nestling age, with breeding pair ID as random factor. I tested all combinations of the explanatory variables (including interactions). The model fit was ranked in accordance with the AICc values as described above.

Finally, for predicting the average prey size being delivered I used prey mass as response variable, I included no fixed effects just the random effect breeding pair ID.

3 RESULTS

3.1 *Prey delivered to the nest*

In total, 187 prey items were recorded delivered by the Ural owl, based on 42 days of filming (Appendix 4). Of the 187 prey items, mammals (52.9 %) was the most frequently delivered prey type, followed by birds (25.7 %), amphibians (12.3 %), insects (3.2 %,) and lizards (0.5 %). Common shrew (48 %) was most prominent prey species by number among the mammals, followed by bank vole (25 %) and field vole (14 %) (Table 1).

The predicted average body mass for prey delivered to the nests, was 40.2 ± 5.8 g (n=192, 5 nests). The total mass recorded delivered at all five nests was estimated to 7596.2 g (Table 1). This amounts to an average of 1519.2 g per nest, and including all prey items consumed by the nestling, the average was 177.7 g per nest per day, and 152.8 g per nestling per day (Appendix 2).

Table 1 : Prey deliveries at the Ural Owl's nests as recorded on video, given the number of prey, mean estimated body mass of each prey group, and estimated mass of each prey group.

Prey type	**Number**	**% by number**	**Estimated body mass (g)**	**Total estimated mass (g)**	**% by mass**
Common shrew	48	25.7	10	480	6.3
Field vole	14	7.5	30	420	5.5
Bank vole	25	13.5	20	500	6.6
Water vole	4	2.1	100	400	5.3
Wood lemming	1	0.5	21	21	0.3
Squirrel	3	1.6	300/251†	802	10.5
Mountain hare	4	2.1	500/418†	1836	24.2
Birds	29	15.5	68*†	2000	26.3
Unidentified bird	19	10.2	36**†	482	6.3
Common grass frog	23	12.3	23	529	7
Common lizard	1	0.5	5	5	< 0.1
Insect	3	1.6	0.2	0.6	< 0.1
Unidentified insect	3	1.6	0.2	0.6	< 0.1
Unidentified prey items	10	5.3	12	120	1.6
Total	187	100.0		7596.2	100.0

* Based on mean weight on 29 birds identified to species

** Based on mean weight on either small or large bird species

† Estimated body mass for decapitated prey items

3.2 *Hunting behavior*

From the models, the predicted probability of prey delivery within an hour block was greater during the night (10 PM – 4 AM) than during the day (Figure 2). The overall predicted probability was 0.17 prey items per hour block of video recording. Between sunset (10 PM) and sunrise (4 AM) the predicted probability was 0.33 prey items per hour block, and between

4 AM and 10 PM the probability of delivery was predicted to be 0.11 prey per hour block (Appendix 2 and 4).

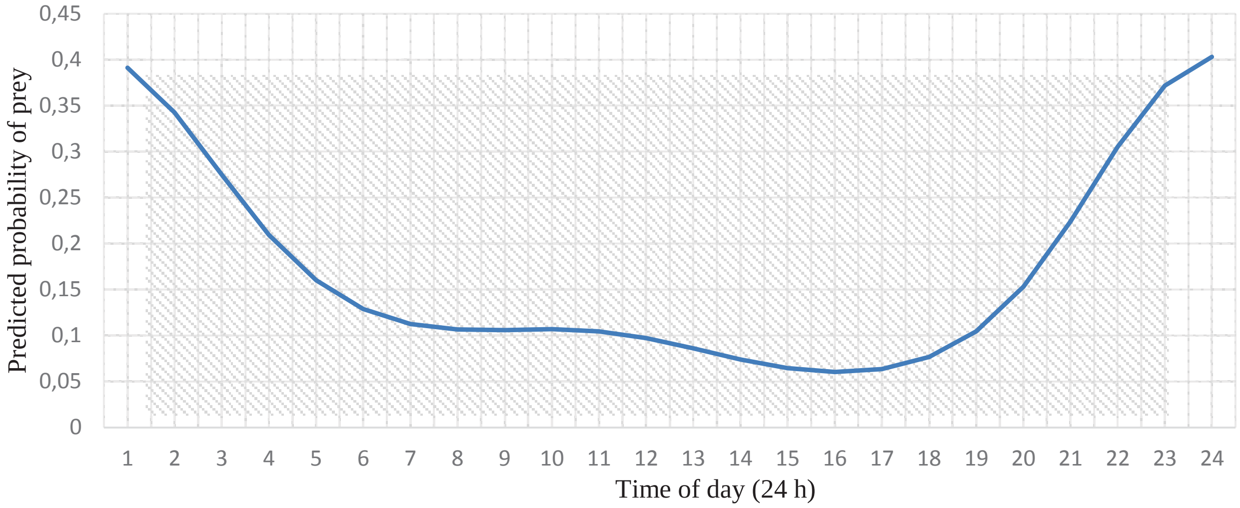

Figure 2: The probability of prey delivery at Ural owl nests as a function of time of day, predicted from models of circadian activity rhythms.

The probability that a bird was delivered to the nest was significantly higher between 11 PM and 2 AM than during the remaining 21 hours of the day (Appendix 10), the predicted average probability of delivery per hour block was 1.5 and 0.04, respectively. For mammals there was no significant differences in predicted probability of delivery throughout the 24 hours, although the probability of a delivery tended to be higher during night than during day, extending longer throughout the morning and increasing earlier in the evening than it did for birds, with an average predicted probability of 0.08 prey items delivered per hour block overall (Figure 3).

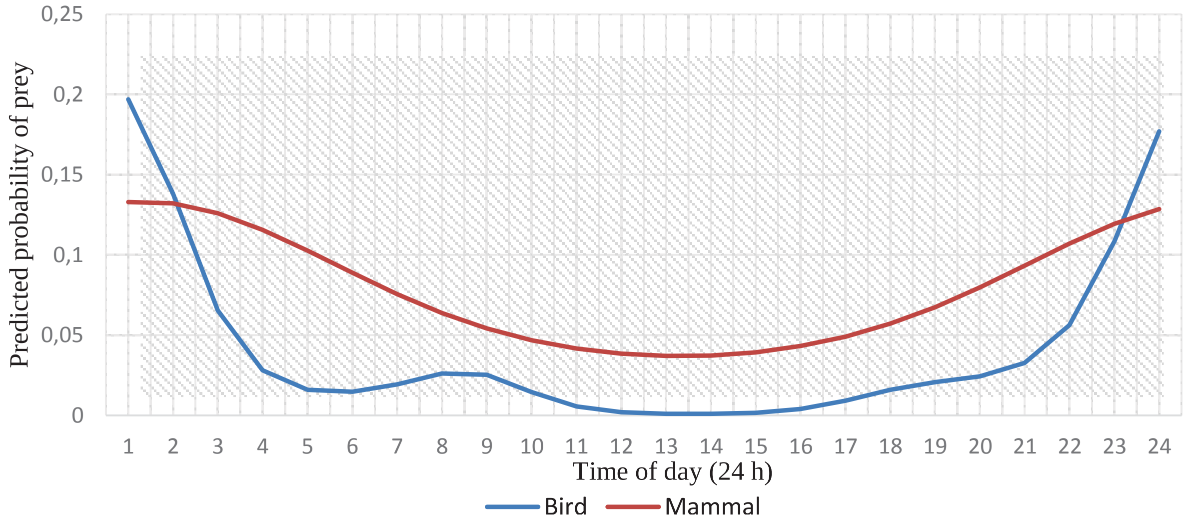

Figure 3: The probability of prey delivery at Ural owl nests as a function of time of day, predicted from models of circadian activity rhythms, separated on mammalian prey (red graph) and avian prey (blue graph).

Among the small mammals delivered, voles and shrews showed a similar pattern, where the predicted probability for delivered voles in particular was highest between midnight and 5 AM. Thus, there was a slight trend that the probability of voles being delivered peaked between 2 AM and 3 AM with, a predicted probability of 0.065 voles items delivered per hour block (Figure 4).

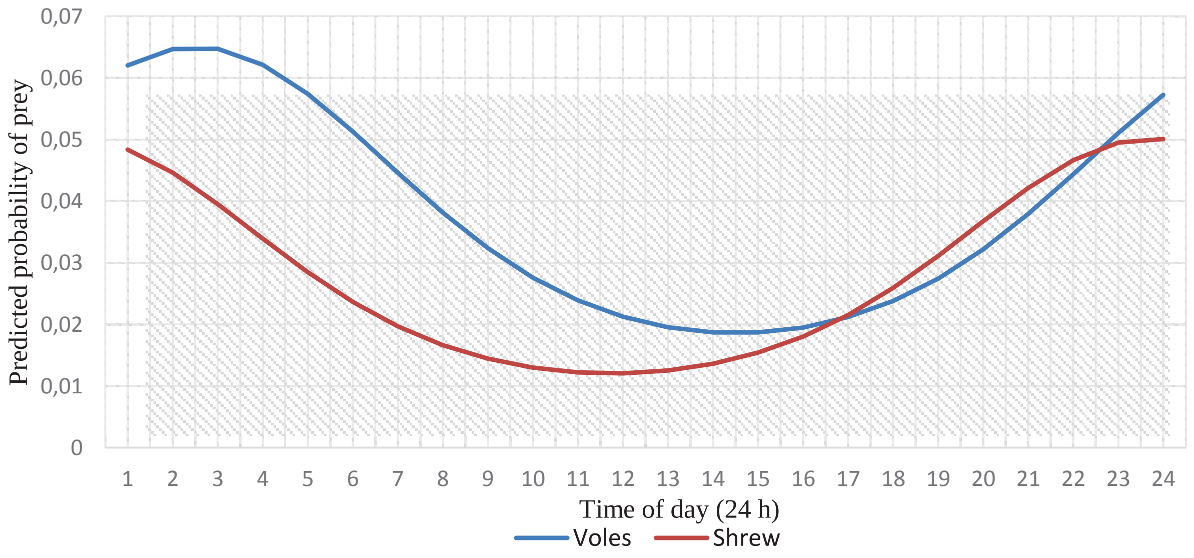

Figure 4: The probability of mammalian prey delivery at Ural owl nests as a function of time of day, predicted from models of circadian activity rhythms separated on shrews (red graph) and voles (blue graph).

3.3 Prey handling in the nest

Of the 187 recorded prey items, 163 were included in the analysis of prey handling in the nest. The female handled 68 (41.7 %) prey items alone, either feeding the nestling (n=65) or feeding herself (n=3). Of these prey items handled by the female, birds (51 %) were the most abundant, followed by mammals (43 %) and amphibians (6 %). The nestling handled 95 (58.3 %) prey items alone. The nestling handled 100 % of the insects and reptiles alone (Appendix 5), 17 % of the amphibians, 69 % of the mammals, and 14 % of the birds (Table 2).

Table 2: Number of amphibians, birds and mammals, handled by the Ural owl female or by the nestlings.

Prey	**Female**	**Nestling**	**Total**
Amphibians	4	16	20
Birds	35	13	48
Mammals	29	66	95
Total	68	95	163

Whether a prey item was handled by a nestling unassisted (Appendix 6) was significantly affected by the age of the nestling and by the prey body mass. The effect of body mass was more significant than the effect of age (Table 3). For prey mass above 100 g the probability that the nestling ingested the prey unassisted was virtually zero, while for prey with lower body mass the probability of unassisted feeding increased with the age of the nestlings (Table 3, Figure 5).

Table 3: Parameter estimates for the significant variables in the model of the probability of Ural owl nestling handling the prey unassisted as a function of prey body mass and nestling age.

	Estimate	**SE**	***z***	***P***
Intercept	-1.07	1.35	-0.78	0.43
Prey body mass	-0.06	0.01	-4.11	<0.0001
Nestling age	0.16	0.07	2.38	0.002

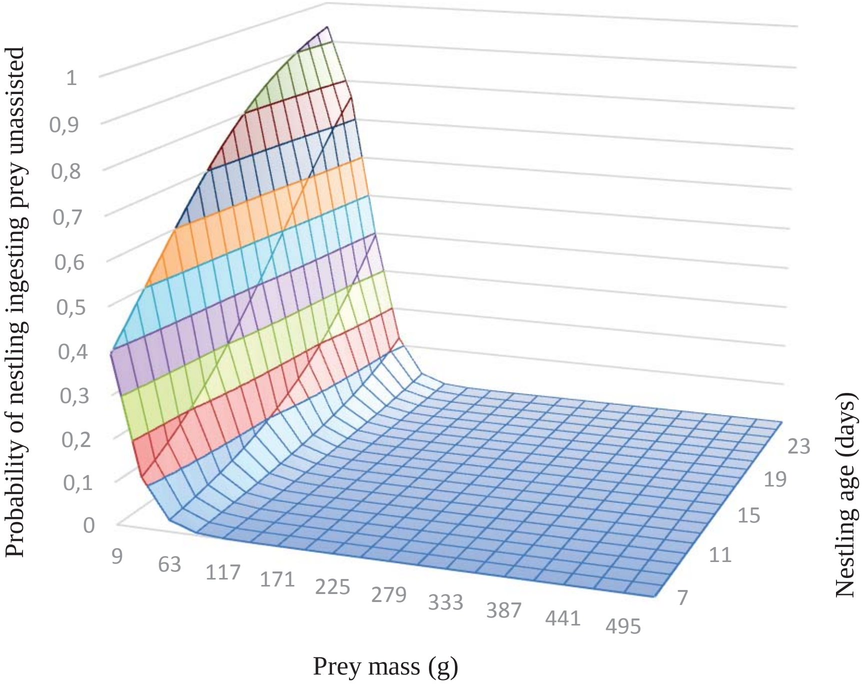

Figure 5: The probability that a Ural owl nestling handled a prey item unassisted, as a function of prey body mass and nestling age.

The interaction between nestling age and prey type, although not significant, was due to the fact that the probability of the nestlings ingesting prey unassisted increased with nestling age and differed between the different prey types. Amphibians and mammals were significantly more likely to be handled by the nestlings unassisted than were birds (Table 4 and 5, Figure 6). For a given prey body mass, the probability of the nestlings handling the prey unassisted was lower for birds than for amphibians and mammals, while there was no significant difference in probability of nestlings handling unassisted between mammals and amphibians (Tables 4 and 5, Figure 6, Appendices 7, 8, 9 and 10).

Table 4: Parameter estimates for the significant variables in the model of the probability that a Ural owl nestling ingested prey unassisted, as function of nestling age, separated on amphibians (intercept), mammals and birds.

	Estimate	**SE**	***z***	***P***
Intercept	- 1.26	1.26	-1.00	0.32
Prey group bird	-3.07	0.76	-4.06	<0.0001
Prey group mammal	-1.08	0.67	-1.60	0.11
Nestling age	0.17	0.06	2.72	0.007

Table 5: Parameter estimates for the significant variables based on the model of the probability that a Ural owl nestling ingested prey unassisted, as function of nestling age, separated on amphibians, mammals and birds (intercept).

	Estimate	**SE**	***Z***	***P***
Intercept	-4.33	1.35	-3.02	0.001
Prey group amphibians	3.07	0.76	4.06	<0.0001
Prey group mammal	1.99	0.50	3.95	<0.0001
Nestling age	0.17	0.06	2.72	0.0061

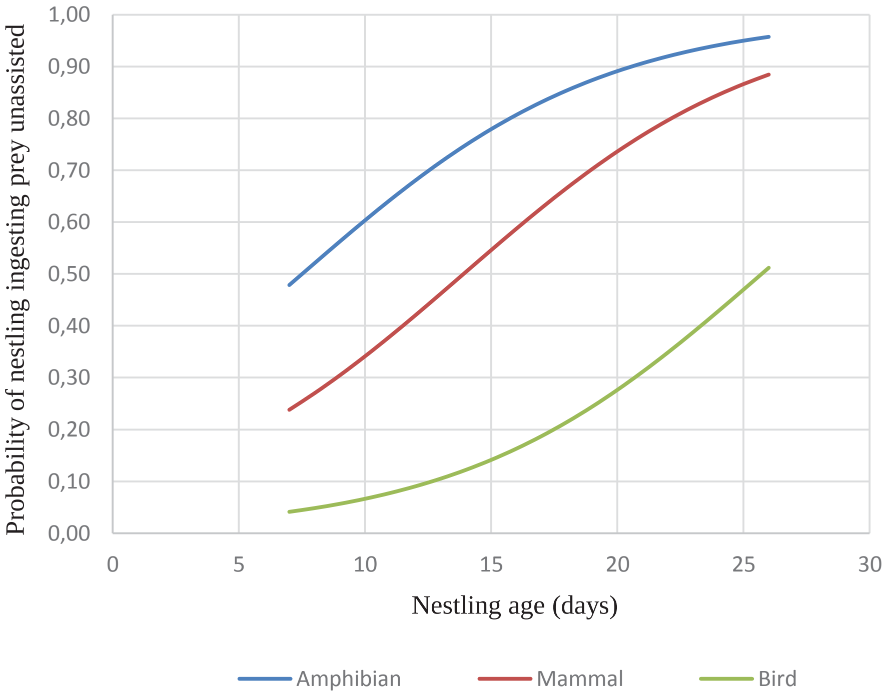

Figure 6: The probability that a Ural owl nestling ingested prey unassisted, as function of nestling age, separated on amphibians, mammals and birds.

4 DISCUSSION

4.1 *Prey delivered at the nest*

In this study Ural owls delivered a fairly wide spectrum of prey at the nest, comprising 52.9 % mammals, 25.7 % birds, 12.3 % amphibians, 3.2 % insects and 0.5 % reptiles. Previous studies based on collection of pellets and prey remains throughout the nestling season have found that the diet varies considerably between years (Lundberg 1981; Jäderholm 1987; Korpimäki & Sulkava 1987; Korpimäki et al. 1990; Sidorovich et al. 2003). Lundberg (1981) found that the Ural owl ate significant more birds (24 % by number and 39 % by weight) and amphibians in a season with low vole abundance. Jäderholm (1987) also found a higher proportion of birds in the diet in one of the three low phases of voles. The portion of birds and amphibians has been found to decrease in seasons with high vole abundance (Lundberg 1981; Korpimäki & Sulkava 1987). Tishechkin (1997) found that the Ural owl in Belarus had a rather specialized diet compared to other European populations of the Ural owl. However, the Ural owl is regarded as a food generalist, where the owl in times of vole scarcity dietary shifts to alternative prey types (i.e. Cramp 1985; Korpimäki et al. 1990).

According to snap trapping, 2008 was a declining year for the abundance of voles in my study area (Geir. A. Sonerud, per. comm.). Optimal foraging theory predicts that in years with low abundance of the preferred prey, the variety of the diet increases (i.e.Pyke 1984). This fits with my results, where bank vole, common shrew, birds and common frog were present as important alternative prey to *Microtus* voles, which are regarded as main prey of Ural owls (Korpimäki & Sulkava 1987, Sonerud 1992). Korpimäki & Sulkava (1987) found that when the proportion of *Microtus* voles in the diet decreased, the Ural owl hunted alternative prey to a greater level. Understanding the Ural owls functional response, i.e. how their prey capture rate is affected by prey abundance (Solomon 1949; Holling 1959) is challenging, because Ural owls utilize several different prey species and because estimating capture rate and prey abundance is infused with methodological challenges (Steen 2010). In addition, both in earlier studies and in the present study, the proportion of alternative prey types in the diet may been over- or underestimated due to the fact that larger prey items are more often delivered at nest and smaller prey items more often consumed at the capture site (Sonerud 1992). Previous studies may have underestimated the importance of prey smaller than *Microtus* voles, whereas the importance of birds, amphibians and water voles may have been overestimated in relation to the functional response to the *Microtus* abundance (Sonerud 1992). In my study, shrews, bank vole and frogs were smaller prey than *Microtus* voles, while birds were larger. Thus, I might have underestimated the proportion of the former, and overestimated the proportion of the latter, compared to what the male really had captured.

4.1.1 Capture of mammals

In my study, mammals (shrews by number and mountain hare by weight) was the prey type most frequently delivered at the nest, but still did not make up more than 53 % of the prey by number. Korpimäki & Sulkava (1987) reported that the diet of the Ural owl consisted mainly of mammals (86 % by number of prey and 87 % by weight), where *Microtus* voles were the most important prey type by number. A similar result was found in another study in Finland (Jäderholm 1987), where voles (92 %) were the most common prey. Additionally, Lundberg (1981) found that voles, especially field voles and water voles, were the most common prey species. By using a video camera directly placed in the nest box Rønning (2007) filmed prey deliveries in seven nests in my study area in 2006, which was a peak year for the bank vole (Geir A. Sonerud, pers. comm.). His study revealed that most prey items delivered by the Ural owls were mammals (73 %), where bank vole (32 %) was the most common prey species, followed by field vole (15 %).

Similar to what Rønning (2007) found, I found that the proportion of bank voles was almost twice as high as that of field voles, and these prey species made up 14 % and 8 % of diet by number, respectively. Rønning (2007) found that bank vole (32 %) was the most important prey by number. Considering that this study was in a peak vole year, a lower proportion of bank vole would be expected if the Ural owl responded functionally to *Microtus* voles only. According to Rønning (2007) the explanation may be that even in a peak year his study area is rather poor, and *Microtus* voles were almost absent. Alternatively, the Ural owl may have a functional response also to bank voles, as found by Korpimäki & Sulkava (1987). In line with this, Lundberg (1981) found that the portion of bank voles consumed by the Ural owl compared to field voles was slightly lower in a decreasing vole year. The primary foods of *Microtus* voles are graminoids and forbs (Hansson 1977), with larger intestines that makes it heavier and slower in the movements than bank voles, who has a varied diet of fruits, seeds and leaves and a smaller intestines (Lee & Houston 1993). In my study the relative abundance of voles was measured by the use of snap trapping. According to Village (1990), this method may not reflect the actual abundance, as some species e.g. bank voles may be easier to trap than others rodent species and trappability may vary between seasons. It is reasonable to think that a Ural owl would easier hunt a *Microtus* voles and that the snap-trapping may not represent the abundance of voles where the hunting took place.

Karell et al. (2010) found that Ural owls captured more field voles than predicted from the trapping data. Bank voles and field voles show marked differences in their social organization. Bank vole females are territorial and dominant over males, while the males form groups in larger home ranges (Viitala & Hoffmeyer 1985). In contrast, field vole males are highly territorial while females have predetermined home range that they do not defend (Myllymäki 1977). Bank voles disperse mainly in a non breeding condition, whereas most field voles disperse when they are in a reproductively active state (Viitala et al. 1994). Younger individuals of Bank voles may be inexperienced in avoiding predators (Longland & Jenkins 1987; Dickman et al. 1991) or because of their low-ranked social status, the younger individuals have to live in poorer and more open habitats (Halle 1988; Meri et al. 2008). Therefore, these differences in the social organization and dispersal behavior inescapably predict differences between species in their vulnerability of predation by Ural owls (Karell et al. 2010).

In my study the Water vole made up only 2 % of the prey by number, but because it is the heaviest vole, its estimated share of prey body mass in the diet of the Ural owls was relatively high at 5 %. Lundberg (1981) found that the Ural owls ate significantly more water voles during the period of decline in voles. Also, Korpimäki & Sulkava (1987) detected a high frequency of water vole when collecting food samples from pellets. Jäderholm (1987) documented that the water vole were the most important prey considering their proportional weight (69%) in the owl’s diet. Water voles are affiliated with riverbanks and agricultural landscape as preferred habitat (Zejda & Zapletal 1969). Considering that my study areas do not contain this type of habitat to any extent, I would expect to find a higher proportion of water voles in areas with higher proportions of agricultural land and riverbanks, i.e. in Finland.

Although mountain hare made up only 2 % of the prey items delivered by the Ural owls, it was in terms of estimated body mass the most important prey species, making up 24 % of the total mass delivered. Mountain hare is considered as an alternative prey species for the generalist Ural owl (Jäderholm 1987; Korpimäki & Sulkava 1987; Sidorovich et al. 2003). The total body mass for mountain hare in my study may however have been overestimated, because it could be assumed that a mountain hare comprises a higher proportion of bones and other body parts that are not consumed than do smaller prey (see Slagsvold et al. 2010).

4.1.2 Captures of shrews

I found that shrews were by number (26 %) the most common delivered prey item, where the majority (71 %) was delivered at on nest (Fastnässatern). Lundberg (1981) found that the proportion of shrews in the diet of Ural owl was low, and concluded that shrews were of little importance, and that the vole abundance did not affect the delivery rate of shrews. However, Korpimäki & Sulkava (1987) noted that the proportion of shrews in the diet of Ural owls increased throughout the breeding season, which indicated that the shrews became more important during the late phase of breeding. Additionally, shrews have an important role as alternative prey in years with decreasing vole abundance (Korpimäki & Sulkava 1987). Shrews are generalists (Saarikko 1989), with an outstandingly high mass-specific metabolic rate (Hanski 1984). Shrews are highly active, and vary between foraging and sleeping in alternate of approximately 46 to 80 min (Saarikko & Hanski 1990). Shrews appear to be neither randomly nor uniformly distributed, the abundance depends on habitat structure (Hansson 1977; Henttonen 1977; Ecke et al. 2002). Both genders of shrews are strictly territorial and defend their territories ferociously (Saarikko 1989; Wang & Grimm 2007). As a result, shrews expose themselves to take risks while foraging when they are in need for food (Barnard et al. 1985). The high daily activity levels (Saarikko & Hanski 1990) and territoriality (Saarikko 1989; Wang & Grimm 2007) may make shrews highly detectable for Ural owls.

4.1.3 Capture of birds

The dominance of birds among prey delivered by Ural owl in my study (26 % by number and 33 % by mass) agrees with an earlier study, where Lundberg (1981) found that birds as a whole were a more frequent prey category during the study period than any single vole species. Korpimäki & Sulkava (1987) reported the proportions of birds delivered among prey recorded in two different areas in Finland to be 10 % by number and 14 % by mass for nests in the Kauhava region, and 9 % by both number and mass for nests in the Keuruu region. As in my study, thrush- and chaffinch-sized species were most abundant, but Korpimäki and Sulkava (1987) showed the utilization of a wide variety of bird species. Additionally, Rønning (2007) also reported that birds constituted a significant part of the delivered prey items, where the proportion of avian prey in the diet was 16 % by number and 32 % by mass.

In contrast, Jäderholm (1987) found a smaller proportion of birds in the diet of breeding Ural owls in Central Finland in 1976-84 (2 % by number and 3 % by mass), possibly because the local habitat conditions did not favor utilization of birds as prey.

Although Ural owls are regarded as nocturnal hunters, they are capable of hunting at day time and because their avian prey are diurnal, it has been assumed that they are for catching birds during daytime (Korpimäki & Sulkava 1987). However, in my study the avian prey was mainly delivered between sunset and sunrise. This pattern was also found by Rønning (2007) in the same study area in 2006; the proportion of birds was at the highest level at the middle of the night and dropped throughout the day. The hunting technique of the Ural owls is similar to that of the Tawny owl (*Strix aluco*), both are for the most part "perch-and-pounce" hunters, where the owl waits for the prey to come into the surrounding area of the chosen perch (Martin 1986). At lower levels of light, the owl must employ auditory localization to detect and locate prey and to capture it unseen (Martin 2012). Thus, powerful vision, and accurate auditory senses together with intimate knowledge of their particularly territory (Martin 2012), provide sufficient information for the Ural owl to be able to hunt birds successfully in the dark, when these prey roost inactively (Lundberg 1979).

4.2 Hunting behavior

Ural owls hunt mainly at night, the hours between sunset and sunrise. I observed that all five owl pairs had a unimodal distribution of the time of day where most prey was delivered, and that the numbers of prey delivered at the nest increases close to the darkest part of the day. It is well known that the Ural Owl is s nocturnal species, but that it also has frequent prey deliveries during twilight (Lundberg 1980a; Lundberg 1980b).

The Ural owl may also be diurnally active, when some prey, e.g. birds, may be more susceptible for predation (Korpimäki & Sulkava 1987). In the present study, some prey was delivered throughout the day, but avian prey was hunted in greatest extent during the darkest periods of the day.

4.3 Food consumption

I found the mean body mass of the prey items to be 41 g. Korpimäki & Sulkava (1987) estimated a higher mean body mass of the prey items; 72 g. In my study each nestlings were estimated to consume on average 153 g/d. In feeding experiments made by Scherzinger (1985) each young consumed 3000 g during the whole nestling period, 30 g per day at the age of 1-5 days and 90 g at the age of 30 days. One reason that I found a higher value may that the prey items, in particular birds and larger mammals, contain parts that can not be ingested (cf. Slagsvold et al. 2010).

In my study prey mass consumed was higher in nests with just one nestling compared with nests with two nestlings. In contrast, Jäderholm (1987) found that number of prey items brought to the nest by the Ural owl increased with the numbers of fledglings. The total prey mass per fledgling is relatively constant in the Tengmalm's Owl (*Aegolius funereus*), whereas the prey mass per fledgling increases steadily from one to four fledglings for the Ural owl. Brommer et al. (2003) found that the total prey mass varied considerably between nests, and that this variation was primarily explained by differences in brood size. In the present study the variation in prey mass consumed for the nest with only one nestling was large (118 g versus 359 g). One possible explanation for this is an overestimation of the mountain hare body mass. The total food need in nest with only one nestling is lower than in nest with two nestlings (Drent & Daan 1980), but if the parents always maximize the total delivery to the brood (Ydenberg 2007), a single nestling should gain more food.

4.4 Prey handling in the nest

In the Ural owls the female delivers almost all the prey to the nestlings, and most of these prey are transferred from the male to the female away from the nest (Cramp 1985). In some cases the male allocates prey items directly to the female inside the nestling box (pers. obs.). Of the prey items delivered at the Ural owl nests that I studied, 58 % were handled by the nestlings unassisted. The nestlings handled all insects and reptiles, 80 % of the amphibians, 70 % of the mammals and 27 % of the birds. The probability that a prey item were handled by the nestlings was influenced by the age of the nestling and by main prey type and prey body mass.

My results indicate that handling by the nestlings was better explained by the body mass of the prey item than by the age of the nestling. A study by Sonerud et al. (2014a) on 9 raptor species found that the female handling assistance declined with increasing age of the nestling, and that the female role as a "food processor" was related to prey size and prey type.

Thus, when the female provisions larger prey, and birds rather than mammals, the female would pay a larger cost by longer handling time and a higher probability of having to assist the nestlings in the prey handling (Sonerud et al. 2014a). Additionally, if the female provides small prey items like insects and shrews that nestling are able to handle themselves, the female have to keep up a higher frequency of prey delivery, i.e. spend more time hunting, to meet the food demand of the nestling (Sonerud et al. 2014b).

There may be several sources of error involved in a comparison of diets between different studies of Ural owl. First, data are obtained in different time periods and habitats, and there is a major difference of the length of these periods and habitat quality (Korpimäki & Sulkava 1987). Second, the methods used for gathering data have changed up through the years. The pellet collection method has primarily been practiced either by collecting pellets in the nest, in the surroundings of nests, or from a stomach sample (Dravecký & Obuch 2009). The new method by using video camera have already been used on some birds of prey, where the study done by Rønning (2007) is the first completed on Ural owl. I would assume that most studies of the diet of raptors in the future will be based on video.

5 CONCLUSION

As predicted from earlier studies the Ural owl is a food generalist, feeding on shrews, bank voles, amphibians and birds as alternative prey types in a year with low abundance of *Microtus* voles. I found that the estimated overall probability of prey delivery at the nest peaked at night between sunset and sunrise, although some prey items were delivered throughout the day. As predicted the handling of prey delivered to the nest depended on nestling age, prey type and prey body mass. Because the probability of nestlings handling prey unassisted increased as they became older and as prey items were smaller the female would be free to hunt rather than dismember prey for the nestling at an earlier stage if smaller prey were provided. On the other hand, this would require a higher rate of small prey delivered to meet the nestlings´ food demand. Being a food generalist adapted to a year-to-year variation in prey abundance, the Ural owl may be better able than many other raptors to cope with future changes in the natural environment posing changes in prey abundance.

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A APPENDIX

Appendix 1: Data on the five nests of Ural Owls filmed in Värmland, Sweden, in 2008.

Locality	Locality name	Latitude	Longitude	Hatching date	Brood size*
1	Hässlingen	60°20′	12°52′	01 May	2
2	Kallbäcken	60°31′	13°16′	10 May	2
3	Väjtjärnen	60°21’	13°11’	12 May	1
4	Svarttjärnen	60°18’	13°16’	14 May	1
5	Fastnässatern	60°13′	13°15′	18 May	1

* Brood size in the end of the monitoring.

Appendix 2: Gross prey mass consumed and number of days monitored in the Ural owl nests.

Nest	Gross prey mass consumed (g)	Days monitored	Gross prey mass per day (g)	Gross prey mass per nestling per day (g)
Hässlingen	580.0	4.95	117.2	58.60
Kallbäcken	1032.0	7.89	130.8	65.40
Väjtjärnen	1028.2	8.73	117.7	117.70
Svarttjärnen	2209.4	12.99	170.1	170.10
Fastnässatern	2746.6	7.79	352.4	352.40
Average	1519.2	8.50	177.7	152.84

Appendix 3: Number and body mass (g) of delivered prey items during video recordings of the five Ural owls nests.

Species	**1**	**2**	**3**	**4**	**5**	**All nests**	**Body mass (g)**	**Body mass sum (g)**
Common shrew (*Sorex araneus)*	4	5	2	3	34	48	10	480
Field vole (*Microtus agrestis*)	2	3	4	0	5	14	30	420
Bank vole (*Clethrionomys glareolus*)	2	3	10	0	10	25	20	500
Water vole (*Arvicola terrestris*)	0	2	0	2	0	4	100	400
Wood Lemming (*Myopus schisticolor*)	0	1†	0	0	0	1	25	21
Squirrel (*Sciurus vulgaris*)	0	0	1†	2†	0	3	300	802
Mountain Hare (*Leptus timidus*)	0	0	0	0	4†	4	500	1836
Sum mammals	8	14	17	7	53	99		
Song thrush (*Turdus philomelos*)	0	1	2	2	0	5	74	370
Redwing (*Turdus iliacus*)	2	0	0	1	0	3	69	207
Fieldfare (*Turdus pilaris*)	1	0	1	0	0	2	105	210
Thrush (*Turdus, sp.*)	0	3	0	3	0	6	81	486
Common chaffinch (*Fringilla coelebs*)	1	1	1	1†	1	5	23	112
Common goldeneye (*Bucephala clangula*)	0	0	0	1	0	1	490	490
Common redpoll (*Carcluelis flammea*)	1	0	0	0	0	1	14	14
Dunnock (*Prunella modularis*)	0	0	0	1	0	1	23	23
Northern Wheatear (*Oenanthe oenanthe*)	0	0	0	1	0	1	22	22
Willow warbler (*Phylloscopus trochilus*)	1†	0	0	0	0	1	10	9
European pied flycatcher (*Ficedula hypoleuca*)	0	1	0	0	0	1	14	14
Pipit (*Anthus, sp.*)	0	0	0	0	2	2	23	46
Unidentified bird, small	0	5†	1	12†	0	18	23	408
Unidentified bird, large	1†		0		0	1	81	71
Sum birds	7	11	5	22	3	48		
Common grass frog (*Rana temporaria*)	3	4	6	4	6	23	23	529
Common lizard (*Lacerta vivipara*)	0	1	0	0	0	1	5	5
Grasshopper (Saltatoria)	0	0	0	0	1	1	0.2	0.2
Owlet moth (Noctuidae)	0	0	0	0	1	1	0.2	0.2
Bettle (Coleoptera, *sp.*)	0	0	0	0	1	1	0.2	0.2
Unidentified insect	0	0	2	1	0	3	0.2	0.6
Unidentified prey items	1	4	0	4	1	10	12	120
Total	19	34	30	38	66	187		7596.2

† Estimated body mass for decapitated prey items. Hässlingen; willom warbler, big bird. Kallbäken; wood lemming, small bird. Väjtjärnen; squirrel. Svarttjärnen; squirrel, small bird, common chaffinch. Fastnässatern; two mountain hares.

Appendix 4: Data on the video recording of the five Ural owls nests monitored in 2008.

Nest	**Onset date**	**Onset hour**	**End date**	**End time**	**Days monitored***
Hässlingen	18 May	14:06:57	23 May	12:55:00	4.95
Kallbäcken	24 May	17:32:00	1 June	14:54:00	7.89
Väjtjärnen	18 May	15:26:00	27 May	08:58:00	8.73
SvarttjärnenA†	27 May	16:26:52	5 June	14:27:00	8.92
Fastnassatern	5 May	12:18:00	13 June	07:19:24	7.79
SvarttjärnenB†	5 June	15:12:00	9 June	16:55:00	4.07

* Number of days monitoring was c. 42 days, where monitoring hours was calculated to c. 992 h.

† Svarttjärnen was monitoring during two periods.

Appendix 5: Number of items of each prey type handled by the female or by the nestlings.

Prey type	**Female**	**Nestling**	**Unknown***	**Total**
Amphibians	4	16	3	23
Bird	35	13	0	48
Insect	0	6	0	6
Mammal	29	66	4	99
Reptile	0	1	0	1
Unknown	9	1	0	10
Total	76	103	7	187

* The feeding session was not recorded, the prey was not eaten or the handling was difficult to view.

Appendix 6: Predicted probability of the Ural owl nestlings feeding unassisted based on the age of the nestlings.

Nestling age	Amphibian	Mammal	Bird
7	0.48	0.24	0.04
8	0.52	0.27	0.05
9	0.56	0.30	0.06
10	0.60	0.34	0.07
11	0.64	0.38	0.08
12	0.68	0.42	0.09
13	0.72	0.46	0.10
14	0.75	0.50	0.12
15	0.78	0.55	0.14
16	0.81	0.59	0.16
17	0.83	0.63	0.19
18	0.85	0.67	0.21
19	0.87	0.70	0.24
20	0.89	0.74	0.28
21	0.91	0.77	0.31
22	0.92	0.80	0.35
23	0.93	0.82	0.39
24	0.94	0.85	0.43
25	0.95	0.87	0.47
26	0.96	0.88	0.51

Appendix 7: Parameter estimates for the significant variables based on predicted probability of mammals being delivered within an hour time block.

	Estimate	SE	z value	P
(Intercept)	-2.567	0.420	-6.108	< 0.001
I(cos(2 * pi * Hour/24))	0.652	0.164	3.973	< 0.001
I(sin(2 * pi * Hour/24))	0.238	0.158	1.503	0.133

Appendix 8: Parameter estimates for the significant variables based on predicted probability of voles being delivered within an hour time block.

	Estimate	SE	z value	P
(Intercept)	-3.316	0.382	-8.660	< 0.001
I(cos(2 * pi * Hour/24))	0.514	0.227	2.259	< 0.0239
I(sin(2 * pi * Hour/24))	0.398	0.223	1.785	< 0.074

Appendix 9: Parameter estimates for the significant variables based on predicted probability of shrews being delivered within an hour time block.

	Estimate	**SE**	**z value**	**P**
(Intercept)	-3.673	0.571	-6.428	< 0.001
I(cos(2 * pi * Hour/24))	0.730	0.231	3.165	< 0.002
I(sin(2 * pi * Hour/24))	-0.047	0.218	-0.215	0.830

Appendix 10: Parameter estimates for the significant variables base on predicted probability of birds being delivered within an hour time block.

	Estimate	**SE**	**z value**	**P**
(Intercept)	-4.028	0.422	-9.548	< 0.001
I(cos(2 * pi * Hour/24))	1.886	0.544	3.468	< 0.001
I(sin(2 * pi * Hour/24))	0.592	0.380	1.557	0.119
I(cos(2 * 2 * pi * Hour/24))	0.137	0.427	0.322	0.748
I(sin(2 * 2 * pi * Hour/24))	-0.506	0.442	-1.146	0.252
I(cos(3 * 2 * pi * Hour/24))	0.468	0.309	1.512	0.130
I(sin(3 * 2 * pi * Hour/24))	0.638	0.336	1.895	0.058

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